

# THE XEROPHYTIC CUCURBITA OF NORTHWESTERN MEXICO AND SOUTHWESTERN UNITED STATES

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The genus *Cucurbita* is indigenous to the American continents. The center of origin probably is the tropical and semitropical regions of southern Mexico (Whitaker and Bemis, 1964). In the hot, arid deserts of northwestern Mexico and southwestern United States there occur a group of xerophytic species, possibly derivatives of populations from mesic ancestors that became adapted to climatic changes toward greater aridity. These species essentially are isolated geographically from other species of *Cucurbita*, and are well adapted to the highly specialized habitat to which they are currently restricted.

The restricted xerophytic species are *C. cylindrata* Bailey, *C. cordata* Wats., *C. palmata* Wats., and *C. digitata* Gray. Although a fifth species, the wide ranging and variable *C. foetidissima* HBK., is truly xerophytic, it is only distantly related to the four restricted species. Another species, *C. pedatifolia* Bailey from central Mexico, has some strong xerophytic characters, and may represent a transitional stage to the xerophytic condition. This paper is concerned with some of the biological characteristics of the restricted species that fit them for their specialized environment and their genetical relationships to each other and to other species of *Cucurbita*.

## RANGE AND HABITAT

These species are confined to the extreme southwestern portions of the United States and adjacent Mexico. This area comprises some of the hottest and most arid locations on the North American continent. The general area is characterized not only by low average rainfall but by relatively prolonged precipitation-free periods; 6 to 10 consecutive months without rainfall are not unusual. At Bahia de Los Angeles in Baja California, Mexico, where *C. cordata* has been collected, a rain-free period of 23 consecutive months has been recorded (Hastings, 1964).

The xerophytic species must be well adapted to their rugged environment in order to survive. These species generally grow in loose, gravelly, well-drained soils below 4,000 feet elevation. The banks or the flood plains of dry, sandy washes are favorite habitats. Such habitats are normally free of stringent competition from other species, and because of their location are likely to receive relatively more moisture than other locations in this uncongenial environment.

Figure 1 shows the range or collection sites of the four species. *Cucurbita cylindrata* is found only in Baja California, mostly in Baja California del Sur, or in about the middle portion of the peninsula. *Cucurbita cordata* has been found only around Bahia de Los Angeles in Baja Cali-

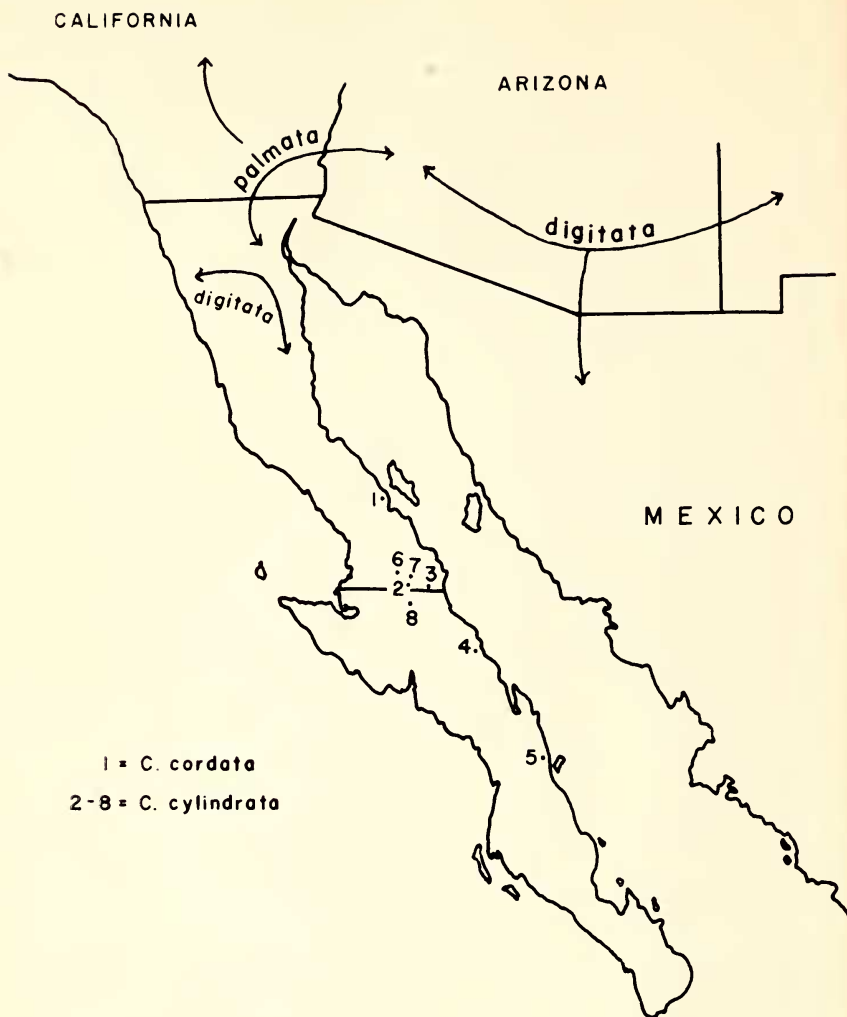


FIG. 1. Distribution of *Cucurbita palmata*, *C. digitata*, *C. cordata* and *C. cylindrata*.

fornia del Norte. It may be that *C. cylindrata* and *C. cordata* are sympatric in the central portion of Baja California. This suggestion, however, requires confirming data from more thorough botanical exploration of the peninsula.

The ranges of *C. palmata* and *C. digitata* are more extensive. *Cucurbita palmata* extends from the northeastern portion of Baja California through California into the San Joaquin Valley and lower portions of the Salinas Valley and eastward to near the Colorado River. *Cucurbita digitata* extends from northern Sonora, Mexico, into southern Arizona and New

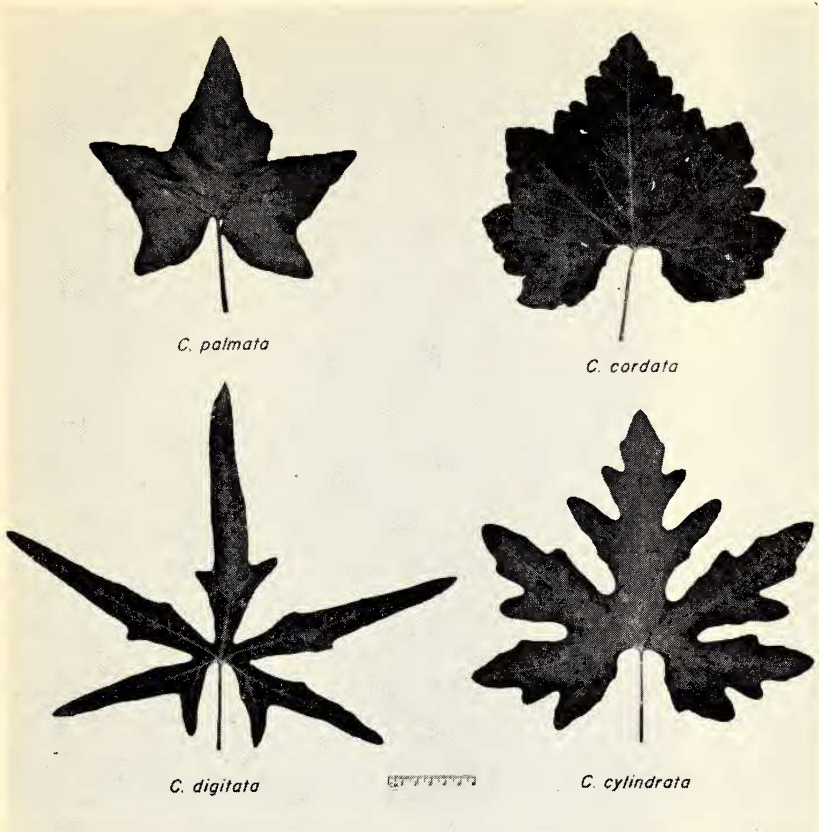


FIG. 2. Typical shape of mature leaves of *Cucurbita palmata*, *C. cordata*, *C. digitata* and *C. cylindrata*.

Mexico. *Cucurbita digitata* also is found at higher elevations in northern Baja California. The ranges of *C. digitata* in southern Arizona and northern Baja California are separated by *C. palmata*. These two species are sympatric at the periphery of their ranges and in these locations interspecific hybridization between them was observed (Bemis and Whitaker, 1965).

#### MORPHOLOGICAL DIFFERENCES

A numerical taxonomic study was conducted by Rhodes, *et al.* (1967) in which 93 plant characters were scored for 21 different species of *Cucurbita*. The four xerophytic species clustered together at a significant level in the eight different statistical techniques that were employed. This indicates a relatively close morphological relationship between them when compared with other species of *Cucurbita*. There are, however, morphological differences among the four xerophytic species.

The most obvious differences among these four species are the shapes of the leaf blades. The first 2 to 4 true leaves of the seedlings (juvenile leaves) are similar in appearance in all four species. The older leaves, however, are quite different (fig. 2). In *Cucurbita digitata* the narrow lanceolate lobes extend almost to the base of the leaf blade; in *C. palmata* the lobes are broad, and about twice as long as they are wide; in *C. cordata* the leaf lobes are again broad extending about one-third the depth of the blade; and finally in *C. cylindrata* the lobes are deep, narrow and obtuse.

There are many other subtle differences between these four species. Among the more marked dissimilarities are the size and shape of the large storage roots. *Cucurbita digitata* has a large turnip-shaped taproot; in *C. palmata* the storage root is stout, fusiform, and bifurcated or even trifurcated a few inches below the crown. *Cucurbita cordata* and *C. cylindrata* each have large fusiform roots. Dittmer and Talley (1964) suggest that the roots of the xerophytic *Cucurbita* are adapted for extracting the moisture from the soil to a depth of not greater than 4 feet. Root penetration is such that there is no possibility of obtaining moisture from deep subsurface water tables. Excluded from this source of moisture, the root system by means of highly developed laterals is well adapted for gathering and storing moisture from the upper 4 feet of soil, and retaining it for an indefinite period of time.

The small gourd-like pepos produced on the vines are similar in shape for each of the xerophytic species, being nearly round. All are distinctly striped but their color patterns differ as follows:

|                      |                      |                        |
|----------------------|----------------------|------------------------|
| <i>C. cylindrata</i> | Dark green           | not yellow at maturity |
| <i>C. cordata</i>    | Gray green           | not yellow at maturity |
| <i>C. palmata</i>    | Diffuse green mottle | yellow at maturity     |
| <i>C. digitata</i>   | Clear green mottle   | yellow at maturity     |

The fresh weight of the pepos range from 150 to 330 grams with *C. cylindrata* usually having the smallest pepos of the four species. The pepo rind is thin, but relatively hard. The narrow band of white flesh is fibrous and when exposed to the desert environment dries into a network of fibers. The pepos are five-carpelate except for *C. digitata* which has three to five with a mean of  $4.5 \pm .8$  carpels. This characteristic of five carpels (consistent for *C. cordata*, *C. cylindrata* and *C. palmata*) is unique in the genus inasmuch as all of the other species of *Cucurbita* are predominantly tri-carpellate. The five carpel character is basically recessive but not completely so because the  $F_1$  hybrids between *C. moschata*  $\times$  *C. digitata* and *C. moschata*  $\times$  *C. palmata* produce pepos with carpel numbers of  $3.4 \pm .6$  and  $3.6 \pm .8$ , respectively. *Cucurbita moschata* Duch. ex Poir. is consistently tri-carpellate (Bemis, 1963).

A single pepo often contains more than 500 seeds. The seeds of *C. cordata* and *C. cylindrata* are smaller than those of *C. digitata* and *C.*

*palmata*. Room dry weight of 100 seeds for the species is  $2.8 \pm .3$ ,  $2.8 \pm .7$  and  $5.4 \pm .5$ ,  $4.9 \pm .7$  grams, respectively. The seed shape and seed coat color are similar for all four species.

The rate of pepo enlargement is rapid for these xerophytic species. The mean diameter of the ovary of *C. palmata* at the time of pollination is 1.6 cm. The rate of enlargement follows a typical sigmoid growth curve which begins to decrease in rate about the 8th day after pollination. The mean maximum pepo diameter of 7.0 cm. was reached on the 12th day after pollination. The rate of seed development (weight), however, is slower than the rate of pepo enlargement. Maximum seed weight is not reached until 34 days after pollination (Ba-Amer, 1967).

#### REPRODUCTION

Observations in the field, experimental garden, and greenhouse suggest that the vegetative method of reproduction in the xerophytic *Cucurbita* is the most common. Each node of a runner is capable of producing adventitious roots, especially if covered with soil. In time the intervening internodes decay. The net result is a group of vegetatively produced plants surrounding a mother plant, and the entire community forms a roughly circular colony. For example, from a single plant of *C. foetidissima* in the experimental garden, a colony of about 705 individual plants was vegetatively produced within the course of three growing seasons.

Our observations in the field suggest that plants of the xerophytic *Cucurbita* regularly produce quantities of ripe fruit with numerous viable seeds, but few seedlings and even fewer mature plants originate from this source. The seeds are an attractive and nutritious source of food for desert animals, particularly rodents. It is evident that only a few seeds survive their depredations. Those that do survive and become young seedlings are vulnerable to browsing mammals, insect attacks, and drought. Thus sexual reproduction is erratic, undependable, and only infrequently results in a mature plant.

The seeds exhibit delayed dormancy apparently associated with the relatively tough seed coat. Some seeds from a mature fruit, properly ripened, will germinate readily, while others do not unless the seed coat is removed. This delayed dormancy may have significance for the survival of the species, but the phenomenon is not well understood.

These observations suggest that the xerophytic *Cucurbita* are adapted to cope reproductively with the rugged environment mainly through a modified version of conventional vegetative reproduction. Such a system allows only limited genetic variation.

#### POLLINATORS

Paul D. Hurd, Jr., and his colleagues have made important monographic studies of squash bees of the genera *Peponapis* and *Xenoglossa* (Hurd and Linsley, 1964; 1966). Females in species of these genera are

specifically dependent upon particular species of *Cucurbita* for their pollen nutrition. Thus species limitation of these insects for pollen becomes a powerful taxonomic tool for studying species relations in the *Cucurbita*. Hurd informs us that it is indeed unusual to find a species-to-species relationship of plants and insects within a single genus of plants. This relationship permits a new approach to the systematics of *Cucurbita*. Already some exciting results are commencing to appear.

Squash bees restricted to *Cucurbita palmata* and *C. digitata* for their pollen supplies are *Peponapis timberlakei*, *Xenoglossa angustior* and *X. strenua*. Hurd has no data for the Baja California species, *C. cordata* and *C. cylindrata*, but he judges from the distribution of squash bees in this area that the same bee species as those dependent upon *C. palmata* and *C. digitata* will also need *C. cordata* and *C. cylindrata* for their pollen economy, with one exception. For those in the southern half of the peninsula, *X. angustior* would be replaced by the endemic *X. mustelina*. As would be expected, a number of species of squash bees are dependent upon the widely ranging *C. foetidissima* as follows: *Peponapis pruinosa*, *P. smithii*, *Xenoglossa angustior*, *X. kansensis*, *X. patricia* and *X. strenua*.

These observations reinforce support for a close relationship between the four xerophytic species from California, Arizona, and Baja California, and the wide divergence of *C. foetidissima* from this group.

#### COMPATIBILITY

The four xerophytic species of *Cucurbita* hybridize readily in all combinations with little if any decrease in fertility in the  $F_1$  plants. The  $F_1$  plants have great vegetative vigor, are self-fertile, and fertile in backcrosses to the parent species.

Where these species are sympatric they tend to hybridize, usually along the perimeter of their range as we have shown for *Cucurbita palmata* and *C. digitata* (Bemis and Whitaker, 1965). It is probable that future botanical exploration in Baja California will uncover a similar situation where the ranges of *C. cordata* and *C. cylindrata* overlap in about the central portion of the peninsula.

The chromosome number of these four xerophytic species is  $n = 20$ . This number is consistent for all species of *Cucurbita* examined thus far. The homology of their respective chromosome complements was verified by cytological examination of *C. cylindrata*, *C. digitata*, *C. palmata* and their reciprocal  $F_1$  hybrids (Groff & Bemis, 1967a). Occasional univalents were observed, but their frequency was the same whether they occurred in a species, or a species hybrid. Hybrids with *C. cordata* were not examined cytologically, but the fertility of the hybrids suggests that its chromosome complement is homologous with the other three species.

Extensive attempts to hybridize these species with other *Cucurbita* yielded few or no seeds. The only success recorded was with *Cucurbita moschata*, a cultivated species, when it was used as the pistillate parent in matings with *C. digitata* and *C. palmata*. The partially developed

embryos from these matings were artificially cultured in order to produce the hybrid plants (Bemis & Nelson, 1963). The hybrids were vegetatively vigorous, but completely sterile. Sixty-three pollen mother cells at MI were examined from the  $F_1$  hybrid *C. moschata*  $\times$  *C. digitata* and the frequency of univalents was  $36.4 \pm 2.9$ ,  $2n = 40$  (Groff and Bemis, 1967b). These observations suggest an almost complete lack of chromosome homology between these xerophytic species and *C. moschata*.

#### BIOCHEMISTRY

Some significant biochemical information relating to the four xerophytic species of *Cucurbita* has been recorded by Chisholm and Hopkins (1966), and confirmed and expanded by Bemis, *et al.* (1967). In a chemical analysis of the seeds of *C. digitata* and *C. palmata* Chisholm and Hopkins found the conjugated fatty acid, punicic acid, in relatively large amounts (17%—*C. digitata*; 11%—*C. palmata*). They state: "*C. digitata* and *C. palmata* are believed to be the only plants native to North America that have been shown to produce punicic acid."

Bemis, *et al.* (1967) added *C. cordata* with 8.99% punicic acid, and a recent analysis of *C. cylindrata* seeds shows this taxon to have 21.4% punicic acid. *Cucurbita foetidissima* had only .36% punicic acid, while in 12 other species of *Cucurbita* the punicic acid ranged from .05% to .33%. This unique occurrence of punicic acid in significant amounts in the seeds of the four xerophytic *Cucurbita* and its virtual absence in seeds of other *Cucurbita*, including the xerophytic *C. foetidissima*, again signifies the close relationship of this group of species.

#### DISCUSSION

The xerophytic *Cucurbita* species, *C. cylindrata*, *C. cordata*, *C. digitata* and *C. palmata* represent an extreme evolutionary divergence in the genus. If our assumption is correct that the center of distribution of *Cucurbita* is the tropical and semitropical region of southern Mexico, then the xerophytic *Cucurbita* are terminal ecotypes adapted and apparently restricted to the hot, dry environments of the deserts in western North America. The evolution of the xerophytic *Cucurbita* from the mesophytic progenitors probably is recent. Evidence for this is that the chromosome number has remained constant, the monoecious character of the plants and the simple inflorescence also have remained constant; but more important is the limited compatibility that still exists with the cultivated species, *C. moschata*.

The morphological characters of the xerophytic *Cucurbita* are either unique for the species or are extreme modifications of certain characters. Among the unique characters are the consistent five-carpelate nature of the pepos with the exception of *C. digitata* which still has some variation. The other species of *Cucurbita* are predominantly tri-carpellate. The pistillate and staminate flowers differ from those of mesophytic species. The pistillate flowers have a pronounced tubular corolla which encloses a long

style with a five-lobed compound stigma. The staminate flowers are also tubular enclosing a long fused anther column.

The flowers are conveniently adapted to protect the solitary squash bees which inhabit the flowers on the day they blossom. The symbiotic relationship between species of *Cucurbita* and certain of the squash bees is unusual. The bees are dependent upon the *Cucurbita* for their pollen nutrition. This need for food from a specific group of plants restricts the distribution of the insects.

The large storage roots of the xerophytic species represent an extreme modification of the tuberculate root of transitional species such as *C. pedatifolia*. The development of the tuberous roots has resulted in the perennial nature of the xerophytic species and the predominantly vegetative mode of reproduction, which in turn restricts the genetic variation because of reduced sexual reproduction. Likewise the relatively high amounts of punicic acid in the seeds found only in the four xerophytic species suggests a close genetic relationship.

The wide ranging *C. foetidissima*, while having xerophytic properties, is not adapted to the extremes of environment of the four species discussed here. Differences in morphological and biochemical characters, specific pollinators, and incompatibility suggest that *C. foetidissima* and the other four xerophytic species diverged at an early date in the evolution of the genus.

The evidence presented in this report probably would lead the trained taxonomist to consider these four taxa as subspecies, if the similarities are considered more significant than the differences between them. In our opinion the subspecies category would be satisfactory.

#### SUMMARY AND CONCLUSIONS

1. *Cucurbita cordata*, *C. cylindrata*, *C. palmata*, and *C. digitata* are adapted to the hot arid regions of the Sonoran desert, primarily through a modification of their root systems.

2. Modification of the root system has led to a change in growth habit from annual to perennial, and to an efficient system of vegetative reproduction which in effect restricts genetic variation.

3. These four species are cross compatible and have many morphological similarities.

4. Two of the four species are specific pollen hosts for three species of squash bees, *Peponapis timberlakei*, *Xenoglossa angustior*, and *X. strenua*. Host specificity of squash bees is a highly sophisticated measurement of relationship among *Cucurbita* species.

5. Certain morphological and biochemical characters unique in the genus separate them from other species of *Cucurbita*. The extreme nature of the habitat they occupy suggests they are terminal ecotypes.

6. Limited compatibility with *C. moschata* relates these species to the annual, mesophytic, cultivated members of the genus.



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